

The Effect of Salinity on Ammonium Sorption in Aquatic Sediments: Implications for Benthic Nutrient Recycling

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ABSTRACT: Ambient exchangeable ammonium concentrations in freshwater sediments are generally considerably greater than those reported for marine sediments. Laboratory measurements indicate that competition for cation exchange sites by ions in seawater is a factor responsible for the lower exchangeable ammonium concentrations in marine sediments. Exchangeable ammonium concentrations were 3- to 6-fold higher when river and estuarine sediments were incubated with fresh water relative to the same sediments incubated with salt water ($\% = 23$). A model was developed to explore the implications for benthic nitrogen cycling of this salinity effect on exchangeable ammonium concentrations. Ammonium diffusion, exchangeable and dissolved ammonium concentrations, and nitrification rates were components of the model formulation. The model output suggests that higher exchangeable ammonium concentrations predicted in fresh water relative to marine sediments can markedly increase the fraction of the ammonium produced in sediments that is nitrified (and subsequently denitrified). These results are consistent with field and experimental laboratory data which indicate that a larger percentage of net ammonium production in aerobic freshwater sediments is nitrified and denitrified (80-100%) relative to marine sediments (40-60%).

Introduction

Sediments are an important site for organic matter decomposition in both freshwater (Hargrave 1973) and marine systems (Nixon 1981). In coastal marine systems substantial amounts of ammonium are released from sediments as a result of organic matter decomposition, providing an important source of nitrogen for phytoplankton production (Nixon 1981; Boynton et al. 1982). In contrast, ammonium released from aerobic freshwater sediments is often negligible (Mortimer 1971; Gardner et al. 1987), although considerable amounts of organic matter are decomposed. The literature on denitrification in freshwater and marine systems indicates that a larger percentage of the ammo-

nium produced during the mineralization of organic N in freshwater sediments is lost from the ecosystem as N_2 as a result of more efficient nitrification, and subsequent denitrification, of ammonium compared to marine sediments (Gardner et al. 1987; Seitzinger 1988a). The mechanism(s) responsible for the higher efficiency of nitrification in freshwater sediments is not known. Recent experimental measurements in this laboratory of the salinity effect on ammonium fluxes from both freshwater and marine sediments showed that "steady state" ammonia fluxes were lower with fresh water flowing over sediments than with salt water flowing over the same sediments (Gardner et al. 1991). These results suggest that some factor

related directly to salinity is regulating ammonium fluxes and nitrification (and denitrification) rates.

Ammonium concentrations are a major factor controlling nitrification rates in aerobic aquatic sediments (Jones and Hood 1980; Henriksen and Kemp 1988). We suggest that mean residence times and concentrations (dissolved plus exchangeable) of ammonium should be lower in marine sediments relative to freshwater sediments, for the same rate of ammonium production, resulting in lower nitrification rates. Lower exchangeable ammonium concentrations in marine sediments are predicted because of competition for exchange sites by the high cation content of seawater and by ion pairing of dissolved ammonium. Theoretically, the amount of exchangeable ammonium in sediments is a function of a number of factors including the ammonium concentration in solution, the ammonium ion activity, as well as the concentration and activity of other exchangeable cations (Berner 1976).

In the present study, we (1) empirically examine the effect of salinity on the amount of exchangeable ammonium in aquatic sediments and (2) develop a model to explore the effect that such differences might have on ammonium concentrations (dissolved and exchangeable), nitrification rates, and the efficiency of nitrification and denitrification in freshwater and marine sediments.

Methods

The surface sediment (ca. 3 cm) was collected in September 1988 from the Barnegat Bay estuary (New Jersey) and the nearby Toms River, which is the major freshwater riverine input to Barnegat Bay. The sediments were collected from Barnegat Bay with an Eckman dredge (water depth 1.5 m) and from Toms River with hand-held plastic coring tubes (water depth 0.1 m). Barnegat Bay is a shallow estuary (average depth 1.5 m) located behind a series of barrier islands. The bottom waters are well oxygenated; salinity at the sediment collection site was 23‰. Sediments collected from the bay were dark brown, silt-clay type sediments. Sediments were collected from the Toms River above any saltwater intrusion and upstream from the drinking water intake for the town of Toms River. The sediments were silty-sand and contained some visible pieces of decomposing leaf litter.

The amount of exchangeable ammonium in sediments incubated with fresh water was measured and compared to the amount in sediments from the same location incubated with salt water using the following method. Twenty milliliters of homogenized sediment from the top 3 cm of either the estuarine or freshwater sediment cores were placed in each of six preweighed plastic bottles

(125 ml). The bottles were loosely capped and placed in an oven at 65°C for 24 h to decrease biological activity. (Previous experiments had indicated that rapid nitrification and denitrification occurred in the bottles if the sediments were not heated.) The bottles were centrifuged at 3,000 rpm for 5 min and the supernatant water was decanted. Three bottles from both locations then received 30 ml each of artificial freshwater (modified from Lehman 1980; Table 1) and three received 30 ml of artificial seawater (modified from Parsons et al. 1984; Table 1; salinity 23‰).

The sediments were resuspended by hand shaking and the bottles were then placed on a shaker table in the dark at 23°C. The water in each bottle was changed daily for 5 d with either fresh or salt water after centrifuging the bottles and decanting the overlying water. On the fifth day, the sediments were equilibrated for 24 h (continuous shaking) with 30 ml of a 100 μ M NH_4Cl solution prepared with either fresh or salt water. The sediments were centrifuged and the ammonium concentration in the supernatant water was measured (Solorzano 1969). The bottles were weighed after decanting so that initial ammonium concentration and volume of water remaining in the sediments could be calculated. The sediments were treated with 30 ml of 2 N KCl solution, shaken for 24 h, and then centrifuged. The ammonium concentration was measured in the supernatant. Sediment dry weight was determined for each bottle and the exchangeable ammonium concentration was calculated based on the difference in the amount of ammonium in solution initially and after extraction with KCl.

The Model

A model of nitrogen cycling in aerobic surface sediments was developed to explore the effect that decreasing exchangeable ammonium concentrations, as caused by salinity changes, might have on the end products of nitrogen mineralization. Model components were dissolved and exchangeable ammonium concentrations, nitrification rates, and fluxes of ammonium and of nitrate plus N_2 across the sediment-water interface. The boundaries of the model were the sediment-water interface and 0.5 cm below the interface. This zone was considered to be aerobic and thus the zone in which nitrification, which requires O_2 , would occur. The depth of this aerobic layer in nature generally ranges from a few millimeters to a centimeter or so in depth (Revsbech et al. 1980, 1986). Ammonium enters this zone of nitrification (z) either by diffusion from ammonium produced below this layer or by production within z ; the sum of these is termed ammonium production (P) and is assumed to be

constant. The model further assumes that there is no net ammonium assimilation into organic matter and that net sediment accumulation is slow relative to the mineralization processes modelled.

The flux of ammonium across the sediment-water interface (F) is modelled according to Fick's First Law of Diffusion as

$$F = -D_s \times dN_d/dz \quad (1)$$

where D_s is the diffusion coefficient for ammonium which includes the effects of tortuosity but not adsorption (Berner 1976), and is equal to $4.8 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$ (Krom and Berner 1980). The term dN_d/dz is the concentration gradient over depth (z) of ammonium in the interstitial water. The concentration gradient which determines the flux of ammonium is the interstitial water concentration gradient, as the flux does not depend on the amount of sorbed species (Duursma and Hoede 1967). In the model, depth (z) is defined as negative; therefore a positive flux is defined as a flux out of the sediments into the overlying water.

The nitrification rate (C) is a function of the average total ammonium concentration in the zone of nitrification (z). The total ammonium concentration is defined as the sum of the interstitial dissolved ammonium concentration (N_d) and the exchangeable ammonium concentration (N_x). The ammonium concentration in the overlying water is assumed to be negligible so that the average total concentration can be approximated as one half of ($dN_d + dN_x$). The nitrification rate, then, is defined as

$$C = Q \times 0.5 \times (dN_d + dN_x) \quad (2)$$

where Q is a constant relating the nitrification rate to the dissolved plus exchangeable ammonium concentration. The validity of this assumption is addressed in the discussion. The value of Q was set equal to $8.3 \times 10^{-6} \text{ cm}^{-1} \text{ s}^{-1}$, in part because it gives a reasonable fit of the model output with the field data.

The exchangeable ammonium concentration (N_x) is defined by the thermodynamic equilibrium constant (K) and by the interstitial ammonium concentration (N_d) as (Berner 1976):

$$K = N_x/N_d \quad (3)$$

The activity coefficient of ammonium was considered to be 1 for purposes of calculation. Therefore, the model did not consider the effect of anion composition and concentration on ion pairing of dissolved ammonium, although this could further enhance the salinity effect on exchangeable ammonium concentrations and nitrification rates by

decreasing the residence time and concentration of ammonium in the oxic layer. The value of N_d is calculated at steady state (i.e., when $dN_d/dt = 0$) from the following equation

$$dN_d/dt = P - C - F - Y \quad (4)$$

where P is the production of ammonium in the sediments, C is the nitrification rate (Eq. 2), F is the flux of ammonium out of the sediments (Eq. 1), and Y is the net flux of ammonium from the dissolved to the exchangeable pool, which is assumed to be rapid relative to the diffusive flux of ammonium. The value of Y is derived from the above equations as

$$Y = 0.5N_d - (0.5(N_d + N_x))/(K + 1) \quad (5)$$

For purposes of calculation the ammonium production rate is set equal to $300 \mu\text{mol m}^{-2} \text{ h}^{-1}$ ($8.3 \times 10^{-6} \mu\text{mol cm}^{-2} \text{ s}^{-1}$), a typical summer value for coastal sediments (Nixon 1981), and sediment porosity is 50%. Model runs were made with K values ranging from 0 to 10. This range was chosen because K values of 1–2 have been reported for coastal marine sediments (Rosenfeld 1979). The ratios of exchangeable to dissolved ammonium calculated for freshwater and marine sediments from literature data (Fig. 1 top) suggest that freshwater K values might generally be 4 or 5 times greater than values for marine sediments (which would put them at about 8 to 10). It should be noted that the ratios calculated in Fig. 1a are not actually K values; K values could not generally be calculated from those data as sediment porosities were not given in many of the studies summarized there. The model was developed using STELLA software (High Performance Systems, Lyme, New Hampshire); results discussed below are for steady state conditions.

The effect of increasing values of K on dissolved and exchangeable ammonium concentrations, nitrification rates, and fluxes of ammonium and of nitrate plus N_2 across the sediment-water interface were explored for three situations: (1) no nitrification, (2) nitrification of only dissolved ammonium, and (3) nitrification of dissolved and exchangeable ammonium. The model calculates the sum of nitrate plus N_2 fluxes as the reduction of nitrate to N_2 by denitrification was not specifically modelled. A large percentage of nitrate produced in sediments is denitrified as shown by ^{15}N isotope studies of nitrification-denitrification coupling (Jenkins and Kemp 1984) and as indicated by comparisons of benthic fluxes of nitrate with denitrification rates (Seitzinger 1987). In the current model it is therefore assumed that most of the nitrate produced is denitrified.

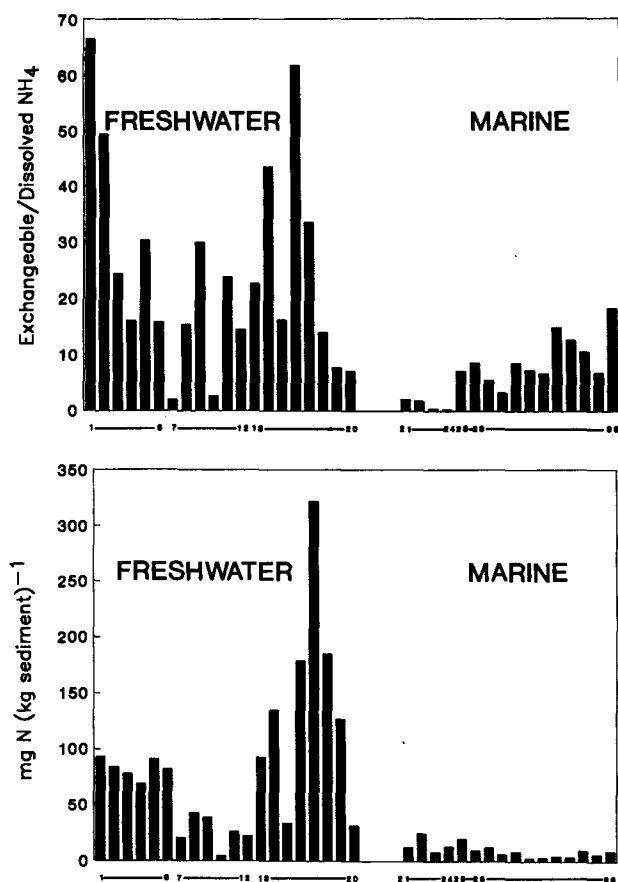


Fig. 1. (top) Ratio of exchangeable ammonium (mg N kg^{-1} dry sediment) to dissolved ammonium (mg N l^{-1} pore water) in a variety of freshwater and marine sediments. Note that these ratios are not equivalent to K values; porosity data were not reported for many sites and thus K values could not be calculated. (bottom) Exchangeable ammonium concentrations (mg N kg^{-1} dry sediment). Data sources: (1–6) Bay Quinte, summer data 0–2 cm and 2–4 cm depths, Liao and Lean 1978; (7–12) Lake Michigan, six sites, Chen et al. 1983; (13–20) lakes Tomahawk, Devils, Crystal, Trout, Little John, Mendota, Monona, and Wingra, Keeney et al. 1970; (21–22) Long Island Sound and (23–24) Florida Bay, Rosenfeld 1979; (25) Narragansett Bay, Garber 1982; (26–36) 11 sites Danish coast, assumed dry sediment density 2.5 g cm^{-3} , Blackburn and Henriksen 1983.

Results

Both river and estuarine sediments had higher exchangeable ammonium concentrations when incubated with fresh water than when incubated with seawater (Fig. 2). Exchangeable ammonium concentrations were 3 to 6.5 times greater in sediments incubated with fresh water than in the same sediments incubated with salt water.

Different model scenarios were run to provide insight into the potential effect of decreasing exchangeable ammonium concentrations due to salinity on dissolved and exchangeable ammonium concentrations, nitrification rates, and sediment-

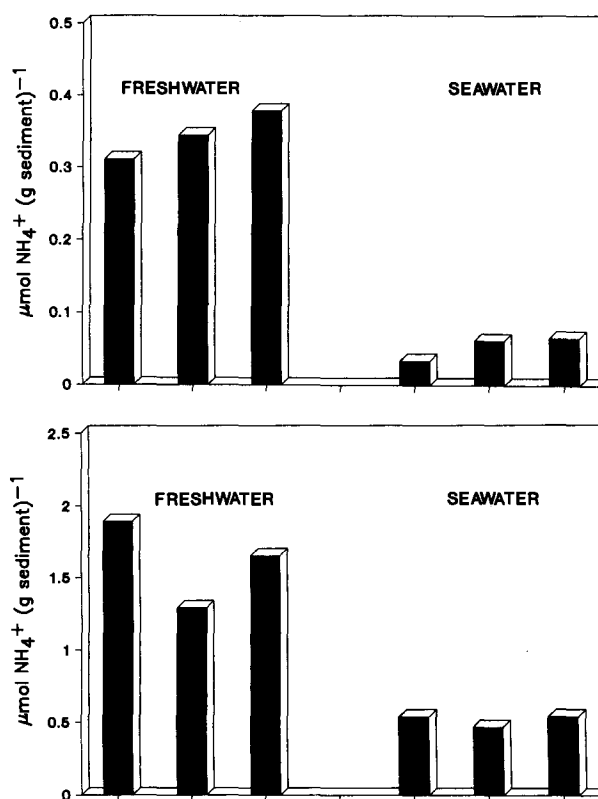


Fig. 2. Exchangeable ammonium concentrations in sediments preincubated for 5 d with either artificial freshwater (three replicates) or artificial seawater (three replicates) and then equilibrated with a $100 \mu\text{M}$ ammonium chloride solution. Sediments from (top) Toms River and (bottom) Barnegat Bay. Units: $\mu\text{mol NH}_4^+$ per g dry sediment.

water fluxes of ammonium and nitrate plus N_2 . In the first case where there is no nitrification ($C = 0$), exchangeable ammonium concentrations increase linearly from 0 to $4.3 \mu\text{mol cm}^{-3}$ dry sediment as a function of K (0 to 10) (Fig. 3 top) and dissolved ammonium concentrations remain constant at $0.43 \mu\text{mol cm}^{-3}$ pore water. (The absolute values of these concentrations and fluxes are, of course, a function of the ammonium production rate and coefficient values used. However, the model-calculated values are presented for comparison of the relative magnitudes of the rates and concentrations under the different scenarios.)

With nitrification of only dissolved ammonium, the exchangeable ammonium concentrations increase linearly from 0 to $3 \mu\text{mol cm}^{-3}$ dry sediment as a function of K (Fig. 3 top). Dissolved ammonium concentrations remain constant, $0.30 \mu\text{mol cm}^{-3}$ pore water (Fig. 3 top). The nitrification rate ($2.5 \mu\text{mol cm}^{-2} \text{ s}^{-1}$) and the flux of ammonium ($5.8 \mu\text{mol cm}^{-2} \text{ s}^{-1}$) also remain constant.

Including nitrification of dissolved and ex-

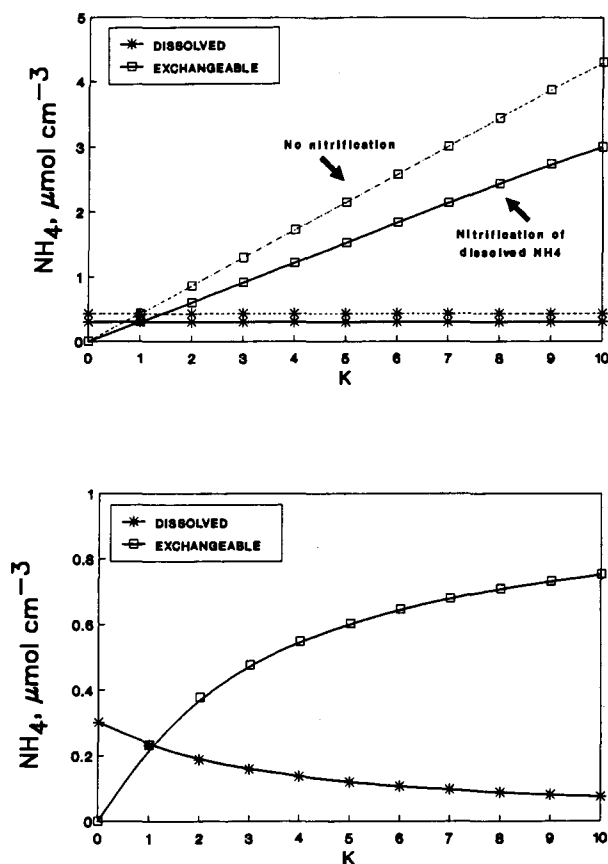


Fig. 3. Model calculation of dissolved ($\mu\text{mol cm}^{-3}$ pore water) and exchangeable ($\mu\text{mol cm}^{-3}$ dry sediment) ammonium vs. K , the ammonium equilibrium constant (top) in the absence of nitrification (---) or with nitrification of only dissolved ammonium (—) and (bottom) with nitrification of dissolved and exchangeable ammonium.

changeable ammonium results in a nonlinear increase in exchangeable ammonium concentrations from 0 to 0.75 $\mu\text{mol cm}^{-3}$ and a nonlinear decrease in dissolved ammonium concentrations from 0.30 to 0.07 $\mu\text{mol cm}^{-3}$ as a function of K values from 0 to 10 (Fig. 3b). Ammonium fluxes decrease and N_2 plus NO_3^- fluxes increase as the value of K increases (Fig. 4). The absolute values of these rates are somewhat affected by the value used for Q ; however, changing the value of Q does not change the general patterns, which are the primary concern here.

Discussion

A number of factors can influence nitrification rates (Henriksen and Kemp 1988) and potentially could be responsible for the differences in nitrification efficiencies in freshwater and marine sediments. Oxygen saturation values are higher in fresh water than salt water and could theoretically

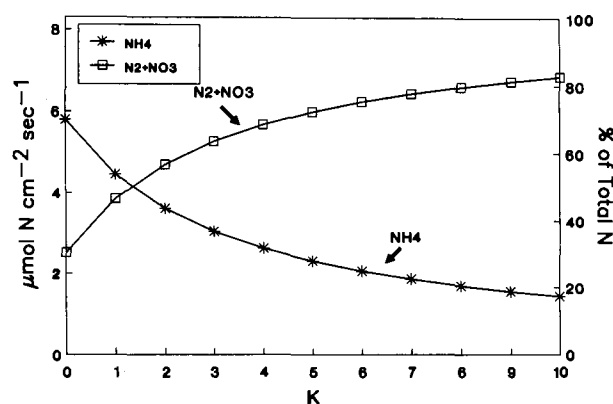


Fig. 4. Model calculation of percent of benthic N flux that is ammonium or N_2 plus NO_3^- , as a function of the ammonium equilibrium constant, K .

result in more oxygen for nitrification in freshwater sediments. However, oxygen saturation values are only about 15% higher in fresh water than saltwater (23‰, 20°C; Weiss 1970), and thus, probably are not responsible for the magnitude of the differences in nitrification efficiencies observed. The pH optimum for nitrification is between 7 and 8.5 (Focht and Verstraete 1977), which is similar to the pH range expected in surface sediments in saltwater environments. Thus, it is unlikely that pH accounts for the lower nitrification efficiencies in saltwater sediments. Nitrification rates by estuarine bacteria acclimated to a range of salinity (0 to 35‰) were similar (Helder and DeVries 1983). Sulfide inhibits nitrification (Srna and Baggeley 1975; Yoshida 1967) and sulfide concentrations are expected to be higher in saltwater sediments than in freshwater sediments due to higher sulfate concentrations in seawater, and therefore, higher sulfate reduction rates. However, the relatively high sulfide concentrations required to inhibit nitrification are not likely to be present in the aerobic surface sediments where nitrification occurs. The effect of sulfide on nitrification warrants further investigation. Nitrification rates are a function of ammonium concentrations and generally follow Michaelis-Menten type kinetics with K_m values typically ranging from 70 μM to 700 μM (Henriksen and Kemp 1988). The experimental measurements and model output reported here, as well as literature data, support our hypothesis that total ammonium concentrations are higher in freshwater sediments than marine sediments, and thus, may be responsible for higher nitrification efficiencies in freshwater sediments.

Data from the literature indicate that exchangeable ammonium concentrations in freshwater sediments are generally higher than they are in marine sediments (Fig. 1 bottom). The ratio of exchange-

TABLE 1. Cation composition of artificial fresh water (AFW) and salt water (ASW) used for incubating sediments to examine the effect of salinity (cation exchange) on exchangeable ammonium concentrations in sediments.

Ion	Concentration, μM	
	AFW	ASW
Na^+	232	308,000
Mg^{++}	82	20,300
K^+		8,100
Ca^{++}	139	1,300

able ammonium (mg N kg^{-1} dry sediment) to dissolved ammonium concentrations (mg N l^{-1} pore water) is also generally higher in freshwater sediments (Fig. 1a). A number of factors can influence the amount of exchangeable ammonium in sediments, and thus could be responsible for the pattern observed here. Exchangeable ammonium concentrations increase linearly with increasing dissolved ammonium concentration in aquatic sediments (Keeney et al. 1970; Rosenfeld 1979). The relative concentration of exchangeable, $N_{(x)}$, and dissolved, $N_{(d)}$, ammonium in sediments is referred to as the thermodynamic equilibrium constant, K:

$$K = N_{(x)}/N_{(d)} \quad (6)$$

Factors that affect K include sediment porosity, clay mineral structure, and organic matter content (Berner 1976). In addition, the value of K depends on the concentration and activities of other cations in solution which compete with NH_4^+ for exchange sites (Berner 1976). The cation concentration of fresh water is hundreds of times less than that of seawater (Table 1) and would be expected to result in generally higher exchangeable ammonium concentrations and higher ratios of exchangeable to dissolved ammonium concentrations in freshwater relative to marine sediments. The effect of ionic strength on interstitial and sorbed ammonium concentrations was noted along a transect in the Potomac River estuary (Simon and Kennedy 1987). However, calculation of the quantitative effect of salinity on K or on the exchangeable ammonium concentrations is difficult considering the complex interactions of numerous cations in seawater and the variation in the clay mineral structure and organic content (Boatman and Murray 1982).

We directly measured the difference in exchangeable ammonium in sediments equilibrated with freshwater and with sea water (23‰). Both river and estuarine sediments had higher exchangeable ammonium concentrations when incubated with fresh water (Fig. 2). Three to 6.5 times more exchangeable ammonium was measured in sediments incubated with fresh water than in sediments from the same location incubated with

salt water. This salinity effect supports the overall pattern of higher exchangeable ammonium concentrations and higher ratios of exchangeable to dissolved ammonium in freshwater compared to marine sediments (Fig. 1 top) found from field data.

The biological implications of this physical/chemical effect of salinity on exchangeable ammonium concentrations was explored using the model presented above. In the simplest case where there is no nitrification ($C = 0$), the dissolved ammonium concentrations are not affected by K (Fig. 3 top). Therefore, the flux of ammonium out of the sediments, which is a function of the dissolved ammonium concentration, remains constant and equal to the production of ammonium ($P = F$). This scenario might be considered to represent lakes or estuaries with anoxic bottom water.

If only dissolved ammonium is assumed to be nitrified, the exchangeable ammonium concentrations increase linearly as a function of K, as in case 1 (Fig. 3 top). However, the exchangeable concentrations are lower than in case 1, because dissolved ammonium concentrations are lower, due to nitrification. Dissolved ammonium concentrations are not affected by K values. Therefore, the nitrification rate and the flux of ammonium, which are only dependent on the dissolved ammonium concentration, are not affected by the value of K. It follows that the percent composition of the benthic N flux remains constant (70% NH_4^+ , 30% $\text{N}_2 + \text{NO}_3^-$) as K increases.

When both dissolved and exchangeable ammonium are assumed to be available for nitrification, there is a marked affect of K on the relative proportions of the end products of N mineralization in the sediments. The model output shows ammonium fluxes decreasing nonlinearly and N_2 plus NO_3^- fluxes increasing nonlinearly as the value of K increases (Fig. 4). Dissolved ammonium concentrations decrease from $0.30 \mu\text{mol cm}^{-3}$ to $0.07 \mu\text{mol cm}^{-3}$ and exchangeable ammonium concentrations increase, but only to $0.75 \mu\text{mol cm}^{-3}$ (Fig. 3 bottom). Note the difference in scale between Fig. 3 top and Fig. 3 bottom. The low dissolved ammonium concentrations at high K values result in small diffusive fluxes of ammonium out of the sediments (Fig. 4). However, nitrification rates increase at high K values, even though dissolved ammonium concentrations are low, because total ammonium concentrations (dissolved plus exchangeable) are higher. The percent contribution of the ammonium fluxes decreases nonlinearly from approximately 50% to 15% of the total nitrogen flux from the sediments (Fig. 4). Fluxes of N_2 plus NO_3^- increased from 50% to 85% of the total nitrogen flux (Fig. 4).

Previous studies of nitrification in aquatic sedi-

ments generally have assumed that only dissolved ammonium was available for nitrification; exchangeable ammonium availability has not been examined (Jones and Hood 1980; Henriksen and Kemp 1988). However, studies in other systems indicate that exchangeable ammonium is available to nitrifying bacteria. For example, ^{15}N isotope studies in soils demonstrated that exchangeable ammonium is available to nitrifiers (Jansson 1958). In dry forest soils ammonium (which presumably is mainly sorbed to exchange sites) is very efficiently nitrified (e.g., Matson and Vitousek 1987). In addition, nitrifying bacteria are generally associated with particles and thus in direct contact with the loosely sorbed, exchangeable ammonium (Kholdebarin and Oertli 1977). These results suggest that both dissolved and exchangeable ammonium are available for nitrification. The inclusion in the model of nitrification of both dissolved and exchangeable ammonium (Fig. 4) reproduces the pattern observed in the field (Fig. 5) of higher nitrification and denitrification efficiencies in freshwater compared to coastal marine sediments. The relative amounts of ammonium, nitrate plus nitrite, and N_2 released from freshwater sediments (lakes and rivers) differ from coastal marine sediments as suggested from a review of data from aquatic systems (Seitzinger 1988a). The primary difference appears to be the percentage of the ammonium that is nitrified. In many freshwater systems with aerobic bottom water, essentially all (80–100%) of the net ammonium produced in the sediments is nitrified and subsequently denitrified (Fig. 5). This contrasts with coastal marine sediments with aerobic bottom waters where only a portion (40–60%) of the ammonium produced is nitrified and denitrified (Fig. 5). The tight coupling between nitrification and denitrification in the sediments results in denitrification of most of the nitrate produced (Jenkins and Kemp 1984).

The experimental measurements of the salinity effect on exchangeable ammonium concentrations (Fig. 2), the model output of nitrification efficiencies as a function of exchangeable ammonium concentrations (Figs. 3 and 4), as well as experimental measurements of the salinity effect on sediment-water ammonium fluxes (Gardner et al. 1991) support our hypothesis that the lower efficiency of nitrification, and subsequent denitrification, of ammonium in coastal marine sediments is due, at least in part, to competition for exchange sites on particles by the high cation concentration of seawater. In addition to this cation effect, anions in seawater would probably form nonpolar ion pairs with ammonium and thereby decrease sorption of ammonium on exchange sites (Gardner et al. 1991). The relative importance of these two phenomena can

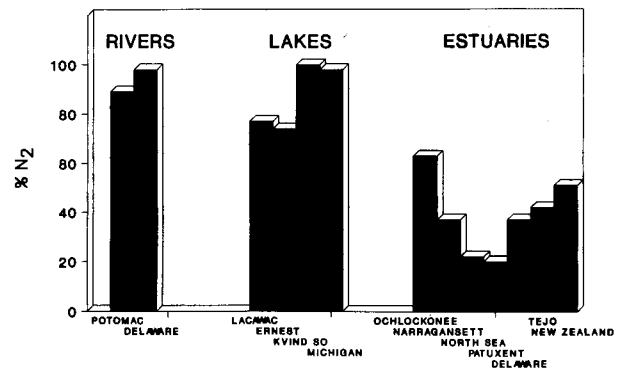


Fig. 5. Percent of sediment-water nitrogen flux that is N_2 (denitrification) in various freshwater and marine systems. Data from Andersen 1971, 1977 (Kvindso); Gardner et al. 1987 (Lake Michigan); Seitzinger 1987 (Ochlockonee Bay); Seitzinger et al. 1984 (Narragansett Bay); Billen 1978 (North Sea); Henriksen and Kemp 1988 (Patuxent); Kaspar et al. 1985 (New Zealand coastal sediments); Seitzinger 1988b (Delaware River); Seitzinger 1988a (Potomac River, Lake Ernest, Lake Lacawac, Delaware Bay, Tejo Estuary).

not be easily differentiated. Studies are now needed to (1) examine directly the relative availability of exchangeable and dissolved ammonium to nitrifying bacteria in aquatic sediments, (2) examine experimentally the effect of exchangeable ammonium concentrations on the relative amounts of ammonium, nitrate, and N_2 released from the sediments, and (3) explore the implications of these findings for nitrogen dynamics in freshwater versus marine ecosystems.

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